

Neural Basis of Disgust Perception in Racial Prejudice

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Abstract: Worldwide racial prejudice is originated from in-group/out-group discrimination. This prejudice can bias face perception at the very beginning of social interaction. However, little is known about the neurocognitive mechanism underlying the influence of racial prejudice on facial emotion perception. Here, we examined the neural basis of disgust perception in racial prejudice using a passive viewing task and functional magnetic resonance imaging. We found that compared with the disgusted faces of in-groups, the disgusted faces of out-groups result in increased amygdala and insular engagement, positive coupling of the insula with amygdala-based emotional system, and negative coupling of the insula with anterior cingulate cortex (ACC)-based regulatory system. Furthermore, machine-learning algorithms revealed that the level of implicit racial prejudice could be predicted by functional couplings of the insula with both the amygdala and the ACC, which suggests that the insula is largely involved in racially biased disgust perception through two distinct neural circuits. In addition, individual difference in disgust sensitivity was found to be predictive of implicit racial prejudice. Taken together, our results suggest a crucial role of insula-centered circuits for disgust perception in racial prejudice. *Hum Brain Mapp* 36:5275–5286, 2015. © 2015 Wiley Periodicals, Inc.

Key words: racial prejudice; disgust; face perception; insula; amygdala; anterior cingulate cortex

INTRODUCTION

The discrimination between “us” and “others” is a fundamental capacity of the human brain [Kubota et al., 2012]. People categorize another individual as “in-group”

or “out-group” within seconds, based on the race, culture, gender, or even trivial characteristics, such as preferences for certain paintings [Simon and Hamilton, 1994]. This in-group/out-group discrimination has been considered as an evolutionary mechanism selected for the advantages of

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group survival [Hewstone et al., 2002]. Importantly, this discrimination results in not only cooperation toward the in-group, but also negative prejudice against the out-group [Amodio, 2014].

The prejudice-related processing toward out-group typically begins with the perception of faces [Brosch et al., 2013], indicated by larger N170 amplitudes to other-race faces [Ito and Urland 2005; Ofan et al., 2011]. It has long been documented that people are relatively poor in distinguishing different faces from other races than from own race, known as other-race effect [Anzures et al., 2013]. Two theories are commonly used to account for such effect [Lieberman, 2007]. One is the perceptual expertise account: more frequent contact with one's own race members leads to more expertised skills to differentiate facial information of its own racial group [Rhodes et al., 1989]. In support of this view, when being asked to intentionally encode different racial face targets, both groups (White and Black) experienced greater fusiform face area (FFA) activation for same-race relative to other-race faces [Golby et al., 2001], or larger N170 following in-group faces [Ratner and Amodio, 2013]. Another theory is the social motivation/categorization account: in-group members are considered as more motivationally relevant or important, therefore leading participants to attend more to them [Hugenberg and Bodenhausen, 2004]. In line with this account, researches found higher FFA activation to faces from motivationally more relevant group, when perceptual experience between the two groups was matched [Van Bavel et al., 2011].

In our opinion, the social motivation account may be more suitable in explaining the influence of racial prejudice on negative facial expressions. For instances, other-race effect can be reversed when other-race faces display cues signaling threat (e.g., angry facial expressions) or power, with higher recognition accuracy for faces from other races than own race [Ackerman et al., 2006; Shriver and Hugenberg, 2010]. In addition, negative emotion from other races is detected more easily, and more likely to be categorized as negative emotions even if facial expression itself is ambiguous [Hugenberg and Bodenhausen, 2003, 2004]. Taken all together, behavioral findings suggest that the perception of racial facial expressions is often inaccurate and biased in the prejudice-consistent direction [Hugenberg and Bodenhausen, 2003, 2004]. However, little is known about the neural mechanism through which racial prejudice influences the perception of emotion on the face. Understanding this mechanism might help to resolve potential misunderstandings and conflicts in social interactions between different races or cultures [Liu et al., in press].

It has been proposed that an amygdala-based emotional system and an anterior cingulate cortex (ACC)-based regulatory system comprise dual neural underpinnings of the racial prejudice [Amodio, 2014]. The amygdala functions to represent an automatically threat-related response to implicit racial bias [Lieberman et al., 2005], whereas the ACC has been associated with an integration of racial bias detection

and the engagement of top-down control in order to inhibit the racial prejudice [Van Nunspeet et al., 2014]. Recently, the insula also has been found specifically associated with participants' implicit negative attitudes toward other-race group [Lieberman et al., 2005; Richeson et al., 2003]. Given that insula is anatomically connected with both amygdala and ACC [Bush et al., 2000], the insula might function as a mediator between the two systems for up-/down-regulating prejudicial affective response [Gu et al., 2013].

Among all negative facial expressions, perception of disgust may be of particular interest, given its close relationship with prejudice [Jones, 2007]. Individuals with higher sensitivity to disgust have been found to exhibit enhanced rejection of out-groups and with a more negative attitude toward homosexuals [Inbar et al., 2009]. Recently, neuroimaging studies have pointed out that processing of disgust signal and prejudice-related information shares neural correlates, such as insula, amygdala, ACC, and orbitofrontal cortex (OFC) [Jones 2007; Kubota et al., 2012]. However, the disgust perception of racial faces and its underlying neural circuits are not yet clearly understood. It would be of particular interest to investigate whether the disgust perception can be modulated by racial prejudice, and whether individuals with different disgust sensitivity differ in this modulation.

In the current study, we examined the influence of racial prejudice on disgust perception and its underlying neural substrates using a passive picture-viewing task with functional magnetic resonance imaging (fMRI). We expected a hyperactive amygdala-based emotional system associated with the facial disgust perception of out-groups compared to those of in-groups. The individual difference in implicit racial prejudice would be predicted by the functional coupling of the insula with both the amygdala-based emotional system and the ACC-based regulatory system. Given that disgust sensitivity is related to increased racial prejudice [Inbar et al., 2009], we also predicted that the influence of racial prejudice on disgusted facial expression is associated with individual difference in disgust sensitivity. Furthermore, a disgust-cued dot-probe behavioral task was performed post-scan to obtain participants' behavioral measures in response to disgusted faces of other races.

MATERIALS AND METHODS

Participants

Thirty-healthy right-handed Chinese students (15 females, mean age 21.7 ± 2.1 years) with normal or corrected-to-normal vision participated in this study. Subjects reported no history of neurological, psychiatric, or endocrine disease, no current use of any psychoactive drugs. None of them had experienced severe physical or emotional trauma. Disgust sensitivity was examined by using the revised Disgust Scale [DS-R, Haidt et al., 1994; Olatunji et al., 2007]. The personality trait was measured

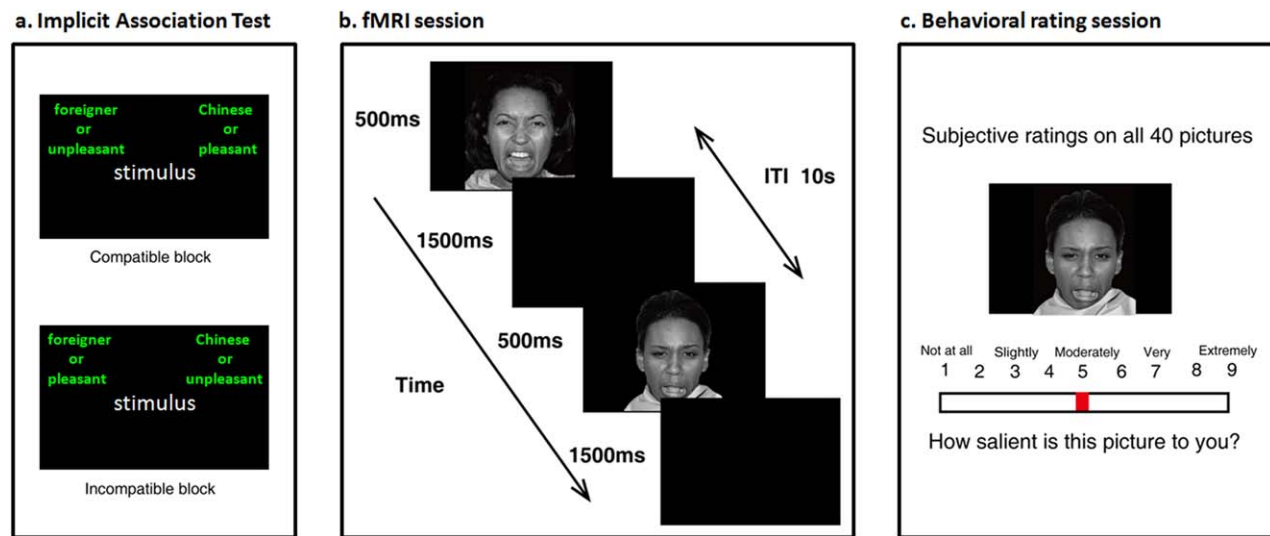


Figure 1.

Experimental design. The experiment consists of three sessions: IAT, passive viewing task, and post-scan testing. (a) During IAT, participants categorized names as “foreigner” or “Chinese” and categorized adjectives as “pleasant” or “unpleasant.” Participants’ implicit racial prejudice was measured by comparing the mean reaction time between two conditions. The compatible condition mapped Chinese names and pleasant adjectives to the same response key while the incompatible condition mapped for-

eigners’ names and pleasant adjectives to the same response key. (b) During passive viewing task, participants underwent fMRI scanning while they were explicitly instructed to passively view the faces presented on the screen without further cognitive processes. (c) During the post-scan testing, participants were asked to rate all facial pictures they had seen in the passive viewing task using a nine-point Likert scale. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

using the Big Five Inventory [John et al., 2008] and the trait/state anxiety was measured using the Spielberger’s Trait Anxiety Inventory [STAI, Spielberger et al., 1970]. Male and female participants were carefully matched for age, disgust sensitivity, personality traits, and trait/state anxiety levels, so to control for the potential influence of gender difference in neural responses to disgust perception and racial prejudice [Caseras et al., 2007; Ekehammar et al., 2003]. The study protocol was approved by the Institutional Review Board for Human Subjects at Beijing Normal University. Informed written consents were obtained from all participants before the experiment. Four participants were excluded from both behavioral and fMRI analyses either due to excessive head movement ($n = 2$, excluding criteria: 2.0 mm and 2.0 degree in max head motion) or other unnecessary cognitive processes involved during scanning ($n = 2$, based on the self-report in post-scan testing, where one reported mind wandering, and the other fell asleep). As a result, the data from 26 participants (13 females; mean age 21.2 ± 1.8 years) were included for further analyses (Supporting Information Table S1). All participants reported no or minimal contact with black people (all participants have not gone abroad, nor have any intergroup contact with African people according to their self reports; only six participants have seen black people in real life).

General Procedure

The experiment was performed between 3:00 and 5:00 p.m., consisted of three sessions (Fig. 1). One hour before entering the MRI scanner, participants were asked to complete an implicit-association test (IAT) to evaluate their implicit attitude toward out-groups. Then they were trained for the passive viewing task, in which they were explicitly instructed to attend to each face appearing on the screen. The fMRI session consisted of 16 blocks in which participants were asked to passively view in-/out-group facial expressions (neutral or disgust). After the fMRI session, participants completed (1) a behavioral rating task, in which they rated all pictures they had seen in the scanner, (2) a self-report questionnaire, which examined whether they had extra cognitive processes during the scanning, and (3) a disgust-cued dot-probe task, which obtained their behavioral performance in response to disgusted faces of other races.

Stimuli

The “group” in this study is defined based on race. Thus Chinese facial pictures represent in-group faces for our participants while foreigners’ facial pictures (only African Americans in this study) represent out-group

faces. Totally, forty faces were used in the current study, including twenty in-group faces selected from the native Chinese Facial Affective Picture System [Gong et al., 2011], and twenty out-group faces selected from the NimStim Set of Facial Expressions (<http://www.macbrain.org/resources.htm>). The forty facial expression pictures showed either neutral or disgusted expressions, with ten pictures in each emotion \times group category (i.e., neutral in-group, disgusted in-group, neutral out-group, and disgusted out-group). The in- and out-group faces were matched on their valence and arousal scores (measured in a nine-point Likert scale) as well as the recognition rates based on a previous survey with a large sample of Chinese participants ($n = 278$) (Supporting Information Table S2). All facial pictures were presented with the same contrast and brightness on the black background ($3.0^\circ \times 3.5^\circ$ visual angle).

Implicit-Association Task (IAT)

Before entering the MRI scanner, participants were asked to perform an IAT in which they categorized ostensibly unrelated words [Hugenberg and Bodenhausen, 2004]. In the compatible trials, participants learned to map Chinese names and pleasant adjectives to one response key ("F" on the computer keyboard), and foreigners' names and unpleasant adjectives to another key ("J"). Then in the incompatible trials foreigners' names and pleasant adjectives were mapped to the "F" key while Chinese names and unpleasant words were mapped to the "J" key. The assignment of keys ("F" or "J") to emotional adjectives and Chinese/foreigners' names was counterbalanced across participants. The adjectives and names used in this study were matched on the number of Chinese characters and strokes between emotions or in-/out-group conditions. The foreigners' names were typical names of African Americans. In the IAT, implicit prejudice is indicated by the extent to which performance in the incompatible trials (i.e., foreigner-pleasant/Chinese-unpleasant) is impaired, relative to the performance in the compatible trials (i.e., foreigner-unpleasant/Chinese-pleasant) [Hugenberg and Bodenhausen, 2004]. The implicit out-group prejudice was defined as the differences of mean response time (RT) between the incompatible and the compatible trials. Notably, the *D* score was also computed using the algorithm described by Greenwald et al. [2003]. Detailed procedure and results are reported in the Supporting Information. The order of incompatible and compatible trials was counterbalanced across participants.

Passive Viewing Task

Participants were instructed to lie down in the MRI scanner and passively view the facial pictures presented on the screen. The faces were presented for 500 ms with an inter-stimulus interval of 1,500 ms [Haxby et al., 2001].

Faces from the same category (i.e., neutral in-group, disgusted in-group, neutral out-group, and disgusted out-group) were presented in oneblock (20 s per block). Each block repeated four times, resulting in 16 blocks in total. Blocks were presented in a pseudo-randomized manner, separated by a 10-s interval. The picture-viewing task lasted for 470 s.

Post-Scan Behavioral Ratings

After the fMRI session, participants were asked to assess the faces on their valence and arousal using a nine-point Likert scale. Same with the result of the previous survey, facial expressions between in- and out-group conditions did not differ in valence and arousal scores (see Supporting Information Table S2). Finally, we asked participants to report their cognitive status during scanning via a brief questionnaire. Two participants were excluded as they reported extra cognitive processes in the passive viewing task (task irrelevant processes, such as mind wandering and fell asleep, which might happen during passive viewing task since no behavioral performance was required).

Post-Scan disgust-Cued Dot-Probe Task

Finally, a disgust-cued dot-probe task was performed to examine selective attention bias to disgusted faces of other race. The specific experimental design was very similar with our previous study [Liu et al., in press], with foreign disgusted faces as cues (50% valid trials). Participants were divided into high and low racial prejudice groups based on IAT scores (median split).

Demographic Data Analysis

Participants' disgust sensitivity was computed in mean scores (total score divided by the number of items). The score of implicit racial prejudice was computed by contrasting the mean RT in the compatible trials with that in the incompatible trials, and divided by 100. Pearson correlation and prediction analysis (linear regression, 4-fold cross-validation, bootstrap with 1,000 times) was performed between the score of implicit racial prejudice and the demographic data (including disgust sensitivity, trait/state anxiety, and personality traits).

Image Acquisition and Preprocessing

Brain image data were collected using the 3-Tesla Siemens TRIO MR scanner in the National Key Laboratory of Cognitive Neuroscience and Learning at Beijing Normal University. Functional images were collected using an echo planar imaging sequence (axial slices, 33; gap, 0.6 mm; repetition time (TR), 2,000 ms; echo time (TE), 30 ms; flip angle, 90° ; voxel size, $3.1 \text{ mm} \times 3.1 \text{ mm} \times 4.0 \text{ mm}$; field-of-view (FOV), $200 \text{ mm} \times 200 \text{ mm}$).

Structural images were acquired through 3D sagittal T1-weighted magnetization-prepared rapid gradient echo (192 slices; TR, 2530 ms; TE, 3.45 ms; voxel size, 1.0 mm × 1.0 mm × 1.0 mm; flip angle, 7°; inversion time, 1,100 ms; FOV, 256 mm × 256 mm). Images were preprocessed using Statistical Parametric Mapping (SPM8; <http://www.fil.ion.ucl.ac.uk/spm>). The first five volumes were discarded for signal equilibrium and participants' adaptation to scanning noise. The remaining images were corrected for slice-timing and realigned for head movement correction. Two participants with head motion exceeding 2.0 mm maximum translation or 2.0° rotation were excluded. Then functional images were co-registered with the T1 weighted 3D image, normalized in MNI space with 3-mm isotropic voxels and smoothed with a Gaussian kernel of 6-mm full-width at half-maximum.

fMRI Data Analysis

Four experimental conditions (neutral in-group, disgusted in-group, neutral out-group, and disgusted out-group) were modeled as separate boxcar regressors and convolved with the canonical hemodynamic response function (HRF) at the first level. Individual's motion parameters from the realignment procedure were included to regress out effects of head movement on brain response. Each normalized image was then high-pass filtered using a cutoff time constant of 128 s. Global intensity normalization and corrections for serial correlations in fMRI used a first-order autoregressive model (AR(1)) in the general linear model (GLM) framework.

A 2 × 2 repeated-measures ANOVA was performed at the second level, with emotion (neutral, disgust) and group (in, out) as two within-subject factors. Significant clusters from the group analysis were initially masked by gray matter mask, and then determined using a height threshold of $P < 0.01$ and an extent threshold of $P < 0.05$, with family-wise error corrections for multiple comparisons based on nonstationary suprathreshold cluster-size distributions computed using Monte Carlo simulations [Nichols and Hayasaka, 2003].

Our primary aim was to examine the interaction between emotion and group effect. Neutral faces in in-group and out-group conditions served as baseline. The contrast of the interaction (i.e., (disgusted out-group–neutral out-group)–(disgusted in-group–neutral in-group)) represents the neural basis underlying out-group bias in disgust perception. Complementary region of interest (ROI) analysis was also performed. The ROIs were selected based on the significant activation clusters in the whole brain analysis of out-group bias. More specifically, the right amygdala (peak at MNI (30, 0, –18)), the right anterior insula (peak at MNI (45, 21, –6)), the right inferior frontal gyrus (peak at MNI (51, 24, –6)), and the left OFC (peak at MNI (–15, 33, –18)) were selected. Parameter estimates associated with the four conditions of interest were extracted from these ROIs at the

individual level using MarsBar (<http://marsbar.sourceforge.net/>) and averaged across voxels within each region. Then the data were submitted for statistical testing, Pearson correlation, and prediction analysis.

Task-Dependent Functional Connectivity Analysis

Given the critical role of insula in disgust perception [Phillips et al., 1997; Wicker et al., 2003] and racial prejudice [Beer et al., 2008; Knutson et al., 2007], we examined the condition-specific modulation of functional connectivity of insula, after removing potentially confounding influences of overall task activation and common driving inputs. The insula seed was anatomically defined using a mask of bilateral insula from anatomical automatic labeling (AAL) template [Tzourio-Mazoyer et al., 2002].

We used a generalized form of task-dependent psychophysiological interaction (gPPI, <http://www.nitrc.org/projects/gppi>), which is much flexible for multiple task conditions in the PPI model [McLaren et al., 2012]. For each subject, the physiological activity of the insula was computed as the mean time series of all voxels within the bilateral anatomical defined mask, deprived from the T contrast of the out-group bias (i.e., (disgusted out-group–neutral out-group)–(disgusted in-group–neutral in-group)) in the first-level GLM analysis. The mean time series from the seed ROI were then deconvolved so as to uncover neuronal activity (i.e., physiological variable) and multiplied with the task design vector to form a psychophysiological interaction vector. This interaction vector was convolved with a canonical HRF to form the PPI regressor of interest. The psychological variable representing the task conditions as well as the mean-corrected time series of the seed ROI were also included in the GLM to remove overall task-related activation and the effects of common driving inputs on brain connectivity. Brain regions showing significant PPI effects were determined by testing for a positive slope of the PPI regressor. Contrast images were then entered into a group level statistical analysis with one-sample t test. The multiple comparison correction was performed as the way described in GLM analysis.

To test our hypothesis that neural responses of disgust processing in racial face perception were associated with individual disgust sensitivity as well as implicated prejudice, we performed multiple linear regressions with the strength of insula functional connectivity as the dependent variable, and disgust sensitivity and implicit prejudice as the predictors. More specifically, the positive connectivity of insula with right amygdala (peaked at MNI (27, –6, –14)), left amygdala (peaked at MNI (–27, –6, –15)), and right fusiform gyrus (peaked at MNI (27, –78, –3)) were selected; the negative connectivity of insula with right ACC (peaked at MNI (3, 45, 13)), and left middle frontal gyrus [defined as dorsal

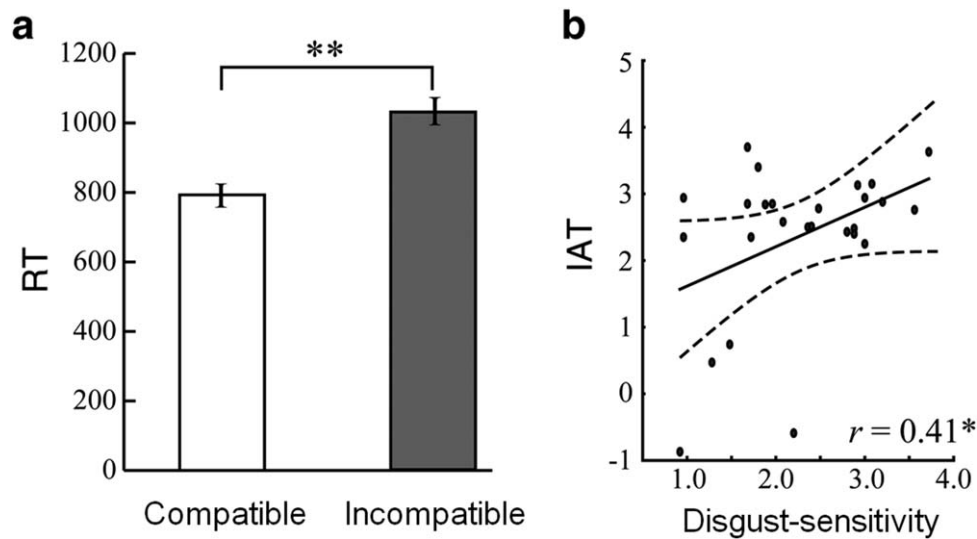


Figure 2.

Scores of implicit racial prejudice and disgust sensitivity. **(a)** Mean reaction time (RT) in compatible and incompatible blocks. **(b)** Individual's disgust sensitivity is a predictor of implicit racial prejudice. Dotted lines indicate 95% confidence intervals. Error bars represent standard error of mean. * $P < 0.05$; ** $P < 0.01$.

later prefrontal cortex, DLPFC, see also Petrides and Pandya, 1999] (peaked at MNI $(-26, -2, 50)$) were selected. Head-motion correlations were computed between disgust sensitivity/implicit racial prejudice, using both conventional root-mean-squared head motion and frame-wise displacement (a frame-by-frame head movement) based on six motion parameters [Power et al., 2012]. None of the correlations was significant ($P_s > 0.3$). The six head motion parameters were entered into the GLM of PPI as covariates to regress out the possible influence of head motion.

RESULTS

Disgust Sensitivity Positively Predicts the Score of Implicit Racial Prejudice

The mean RT in the incompatible trials (1029.05 ± 204.84 ms, mean \pm SD) was significantly higher than that in the compatible trials (792.82 ± 160.36 ms, $t(25) = 10.47$, $P < 0.001$) (Fig. 2a), indicating an implicit prejudice against out-group. Interestingly, we found a significantly positive correlation between individual's disgust sensitivity and the score of implicit prejudice ($r = 0.41$, $P = 0.035$; Fig. 2b). Using machine-learning algorithms with cross-validation, we confirmed that individual's implicit prejudice could be reliably predicted by disgust sensitivity ($r_{(\text{predicted}, \text{observed})} = 0.30$, $P = 0.038$). Neither trait/state anxiety nor personality traits showed robust relation to implicit prejudice ($P_s > 0.2$),

which was consistent with previous studies [Inbar et al., 2012; Navarrete and Fessler, 2006].

Engagement of Amygdala and Insula in Prejudicial Disgust Perception

We compared brain activations of disgusted versus neutral faces averaged across in-/out-group conditions. Increased activation in the bilateral anterior insula, inferior frontal gyrus, and fusiform gyrus was found for disgusted faces than for neutral faces (Supporting Information Table S3 and Fig. S1), which was consistent with previous neuro-imaging studies in disgust [Phillips et al., 1997; Wicker et al., 2003]. Compared with in-group faces, greater neural responses of amygdala and visual cortex were found for out-group faces (Supporting Information Table S4 and Fig. S2). No significant results were found in either the contrast of neutral versus disgust or the contrast of in-group versus out-group.

More importantly, the contrast of the interaction (i.e., (disgusted out-group–neutral out-group)–(disgusted in-group–neutral in-group)), which represents the neural basis of out-group bias in disgust perception, revealed significant activation in the right amygdala, insula, and inferior frontal gyrus, as well as in the left orbital-frontal cortex (Fig. 3a,c, Table I, Supporting Information Fig. S3). Follow-up ROI analysis confirmed that individual's disgust sensitivity can positively predict the activity in the amygdala ($r_{(\text{predicted}, \text{observed})} = 0.38$, $P = 0.010$, Fig. 3d), and in the insula ($r_{(\text{predicted}, \text{observed})} = 0.38$, $P = 0.007$, Fig. 3b),

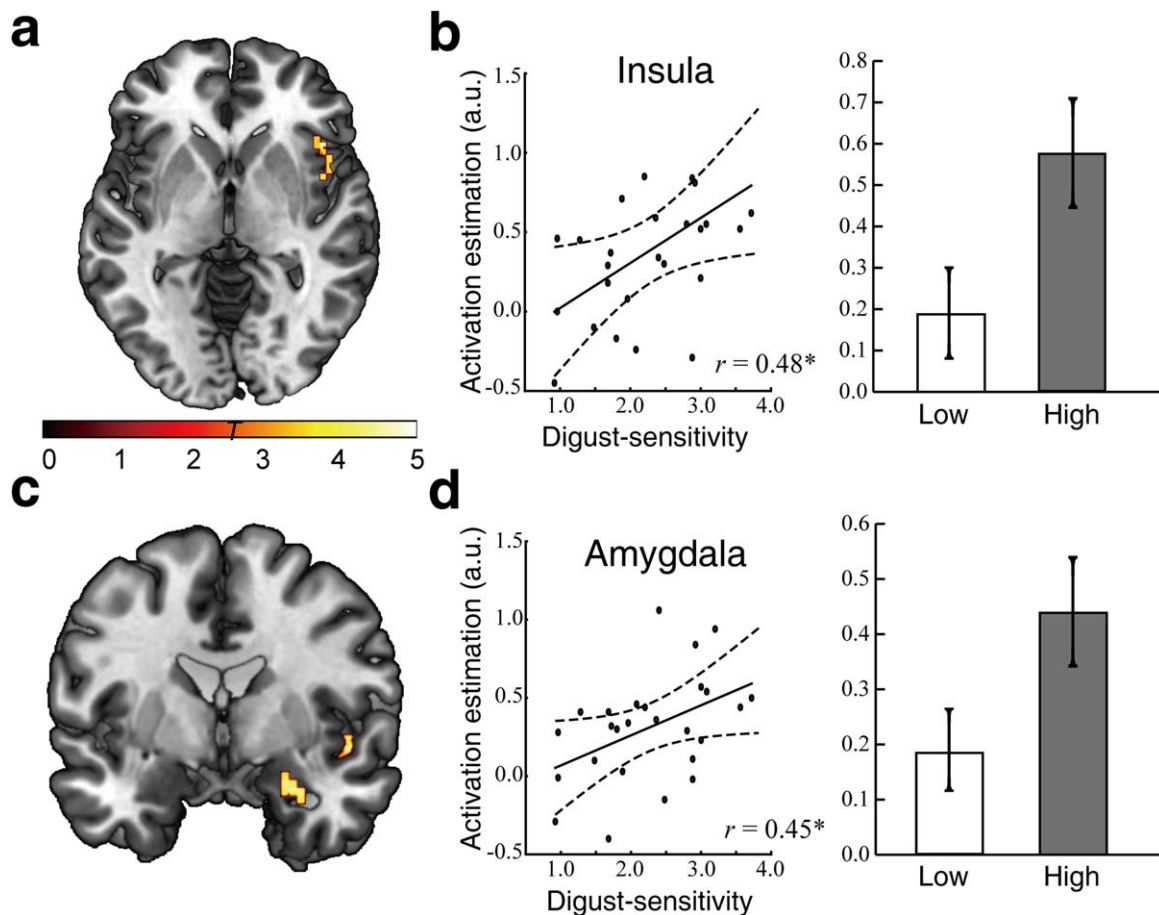


Figure 3.

Insula and amygdala underlying the racial prejudice in disgust perception and their relations to disgust sensitivity. (a, c) Axial view of right anterior insula and coronal view of right amygdala engagements that underlie theracial prejudice in disgust perception (i.e., (disgusted out-group – neutral out-group) – (disgusted

in-group – neutral in-group)). (b, d) Higher disgust sensitivity is predictive of greater activations in the right anterior insula and the right amygdala. Bar graph represents the median split in disgust sensitivity. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

which was in line with previous studies [Calder et al., 2007]. No significant results were found in the reversed pattern (i.e., (disgusted in-group–neutral in-group)–(disgusted out-group–neutral out-group)). Neither the activation of the amygdala ($r_{(\text{predicted}, \text{observed})} = 0.18$, $P = 0.39$) nor the insula ($r_{(\text{predicted}, \text{observed})} = 0.20$, $P = 0.32$) was predictive of individual's implicit prejudice.

Prejudice in Disgust Perception is Characterized With Increased Positive Coupling Between Insula–Amygdala and Negative Coupling Between Insula–ACC

With the out-group bias in disgust perception as the psychological context and the blood-oxygen-level depend-

ent (BOLD) signal of the anatomical defined insula as the physiological signal, PPI analysis showed that the neural activity in insula was positively coupled with the bilateral amygdala while it negatively coupled with the right ACC (Fig. 4a,b, Table II).

More importantly, multiple linear regressions, with the strength of insula functional connectivity as the predictors, and disgust sensitivity and implicit racial prejudice as the dependent variables, revealed that insula–amygdala functional connectivity positively predicted individual levels of both disgust sensitivity and implicit racial prejudice; at the same time, insula–ACC functional connectivity negatively predicted both disgust sensitivity and implicit racial prejudice (Table III). Insula seed functional connectivity with all other brain regions cannot predict disgust sensitivity or implicit racial prejudice ($P_s > 0.2$).

TABLE I. Brain activation of the racial prejudice in disgust perception during the passive viewing task ((disgusted out-group–neutral out-group)–(disgusted in-group–neutral in-group))

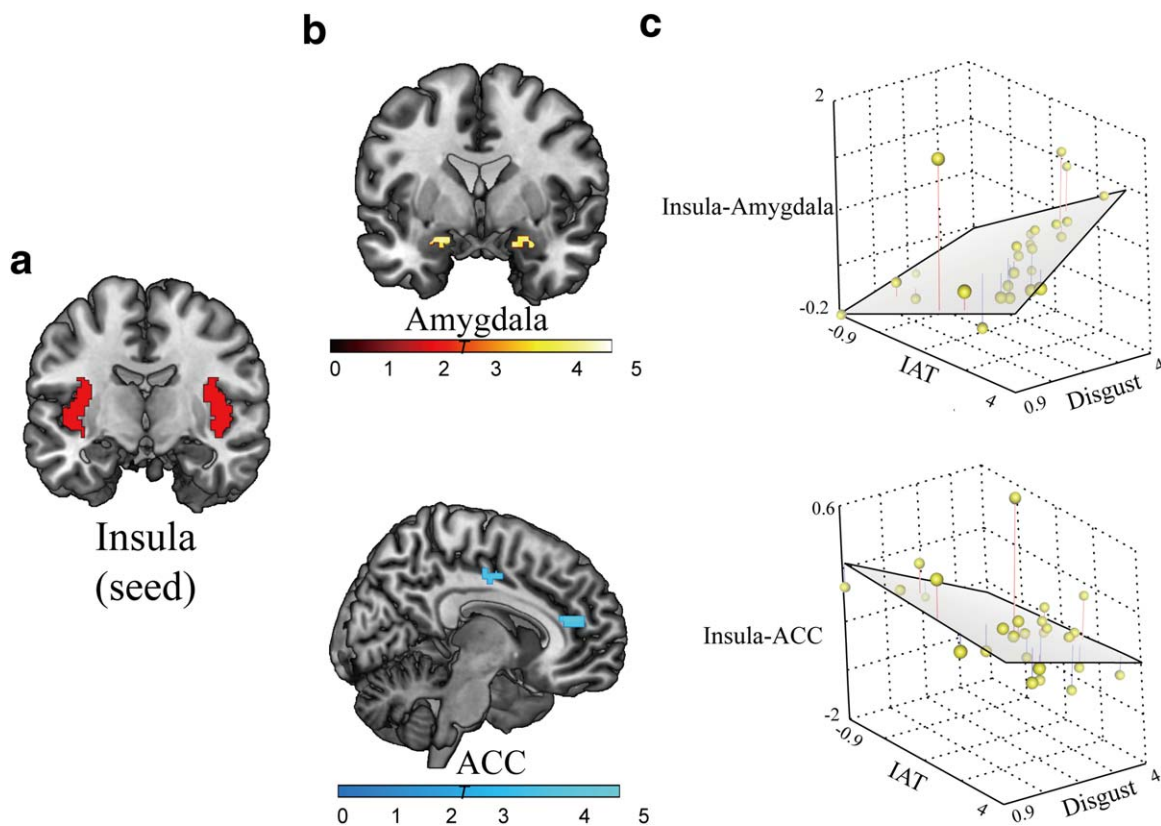
Brain regions	L/R	BA	<i>T</i> values	Coordinates (<i>x,y,z</i>) (MNI)		
Amygdala	R	—	4.57	30	0	–18
Insula	R	—	4.07	45	21	–6
Orbital frontal cortex	L	47	3.19	–15	33	–18
Inferior frontal cortex	R	47	4.95	51	24	–6

L, left; R, right; BA, Brodmann's area.

Complementary Behavioral Evidence

The results of disgusted-cue dot-probe task showed that, compared with low prejudice group, the RT of high prejudice group was significantly shorter in valid trials (high

prejudice = 312 ms, low prejudice = 390 ms, $t(24) = 3.68$, $P = 0.002$), but significantly longer in invalid trials (high prejudice = 402 ms, low prejudice = 344 ms, $t(24) = 2.40$, $P = 0.025$). No significant difference between groups was found in accurate rates ($P_s > 0.7$).

**Figure 4.**

Functional connectivity of insula under the racial prejudice in disgust perception. (a) Coronal view of the anatomically defined bilateral insula used as seed in psychophysiological interaction analysis of task-based functional connectivity underlying the racial prejudice in disgust perception (i.e., (disgusted out-group – neutral out-group) – (disgusted in-group – neutral in-group)). (b) Coronal view of bilateral amygdala (in hot) and sagittal view

of right ACC (in cool) showing increased functional connectivity with insula. Hot denotes positive coupling and cool denotes negative coupling. (c) Correlations among functional connectivity of insula and amygdala/ACC, implicit racial prejudice, and disgust sensitivity. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE II. Functional connectivity of insula underlying the racial prejudice in disgust perception

Brain regions	L/R	BA	T values	Coordinates (x,y,z) (MNI)		
Positive connectivity						
Amygdala	R	—	3.10	27	−6	−14
	L	—	3.22	−27	−6	−15
Fusiform gyrus	R	37	4.45	27	−78	−3
Middle occipital gyrus	R	18	3.67	30	−84	9
	L	18	3.23	−30	−93	−3
Inferior occipital gyrus	L	18	2.69	−30	−87	−4
Inferior temporal gyrus	L	36	2.73	−39	−24	−21
Thalamus	L	—	3.25	−21	−18	9
Negative connectivity						
Anterior cingulate cortex (dorsal)	R	32	3.75	3	45	13
Anteriorcingulate cortex (ventral)	R	24	3.42	6	−9	42
	L	24	3.38	−6	−18	42
Middle frontal gyrus	L	6	2.76	−26	−2	50
Superior temporal gyrus	R	22	4.12	60	6	0
Cerebellum	L	—	4.07	−12	−30	−45

DISCUSSION

Our results corroborate that racial prejudice does affect facial perception of disgust. The neuroimaging data tend to support the social motivation account rather than the perceptual expertise theory, because while the participants had much more experience with in-groups than out-groups, the perception of out-group faces (compared to in-group faces) evoked higher activation in visual cortex (e.g., FFA). This result is consistent with previous findings that people treated out-group faces as threat-related signals, and allocated more attention to them [Ofan et al., 2014]. It was also found that out-group faces evoked more activity in FFA and amygdala [Amodio et al., 2003; Lieberman et al., 2005], and the difference of amygdala activity between out-group and in-group faces was positively correlated with the implicit racial prejudice to out-groups [Phelps et al., 2000]. One promising explanation according to the social motivation account is that, when racial prejudice was evoked, participants considered out-group members as more motivationally relevant or important, and thus resulting in more attention to them, regardless of prior experience [Ofan et al., 2014]. However, the current results do not necessarily contradict with the perceptual expertise theory. It is possible that the lack of experience with Black people was the reason for the higher activation of FFA and amygdala in response to out-group faces,

because it has been found that unfamiliar faces may elicit novel neural responses [Balderston et al., 2011; Wright et al., 2003].

The main finding of the current study is that racial prejudice influences disgust perception via two distinct neural processes. On the one hand, amygdala-centered emotion circuit is the core neural mechanism underlying threat-related responses [Bishop et al., 2004]. As the hub of emotion-processing network, amygdala receives direct afferents from various sensory organs into its lateral nucleus, enabling itself to respond very rapidly to immediate threats. Strengthened functional connectivity between insula and amygdala in response to racial disgusted faces may bias the perception of emotion and make observers consider the disgusted faces as with more salient threats. In line with this argument, the positive coupling between insula and amygdala is predictive of individual's implicit racial prejudice in the current study.

On the other hand, the increased negative insula-ACC coupling when viewing out-group disgusted faces may indicate a failure in deliberate cognitive regulation or in the inhibition of prejudicial responses [Amodio et al., 2008; Bartholow, 2010]. For instance, low-prejudice participants exhibited better control on a stereotype-inhibition task, accompanied by stronger neural responses associated with conflict monitoring [Amodio et al., 2008]. The ACC is

TABLE III. Correlation and prediction analysis of insula functional connectivity in relation to disgust sensitivity and implicit racial prejudice.

Brain regions	Disgust sensitivity		Implicit racial prejudice	
	Correlation	Prediction	Correlation	Prediction
Insula-Amygdala	0.58 (0.002)	0.46 (0.007)	0.46 (0.017)	0.38 (0.016)
Insula-ACC	−0.42 (0.032)	0.34 (0.020)	−0.50 (0.009)	0.37 (0.026)

essential for inhibition function [Etkin et al., 2011] and is responsible for top-down control of amygdala activity [Ochsner and Gross, 2005]. Even in the absence of explicit instructions for cognitive control, the ACC activation has been consistently reported to increase when participants passively view other-race (relative to own-race) faces, suggesting that the ACC is spontaneously involved to prevent or regulate the unwanted influence of implicit prejudice [Lieberman et al., 2005; Richeson et al., 2003]. Previous studies have revealed that the conflict between automatic, prepotent feelings (such as disgust or fear), and conscious intentions to respond fairly may activate ACC [Blair and Banaji, 1996]. For example, when European Americans view the faces of European and African Americans, increased activation in the ACC correlates with reduced activation in the amygdala, indicating an emotion regulation circuit between the two regions [Richeson et al., 2003]. The current finding suggests that the racial prejudice is also shaped, at least partially, by strengthened negative coupling between insula and ACC-based regulatory neural system. Taken together, both the strengthened positive coupling of the insula with the amygdala-based emotion system and the enhanced negative coupling of the insula with the ACC-based regulatory system underpin disgust perception in racial prejudice.

Furthermore, results of the disgust cued dot-probe task provide direct evidence for stronger attentional bias to disgusted faces of other-race. The faster reactions of high prejudice group in the valid condition indicate a significant attention orienting triggered by disgust perception, whereas the slower responses in the invalid condition suggest a failure to disengage visual attention from disgust/threats or a defective regulatory process. Though the behavioral result is not able to provide evidence of amygdala or ACC recruitment, or rule out other alternatives, it at least partially supports our hypothesis that human racial prejudice can bias their perception of facial expressions from other-race members.

In addition, individual difference in disgust sensitivity is found to be predictive of the level of implicit racial prejudice. According to the hypothesis of “behavioral immune system” [Curtis et al., 2011], higher disgust sensitivity reflects a more readily behavioral immune system, i.e., a stronger desire to avoid the contamination rooted in the emotion state of disgust [Schaller and Park, 2011]. Although the correlation analysis here cannot infer causality, the observed relation between disgust sensitivity and racial prejudice might be interpreted to be associated with the disgust function of avoiding contamination in the social context [Curtis et al., 2011], since racial out-groups may pose threat of foreign diseases or impurity [Inbar et al., 2012]. Such desire of avoiding contamination is in line with the evolutionary purpose of racial prejudice, i.e., to facilitate in-groups’ survival by distancing out-groups [Cottrell and Neuberg, 2005]. Similarly, recent studies found a positive correlation between disgust sensitivity

and political conservatism [Inbar et al., 2012]; the neural responses to a single disgusting image can largely predict individual’s political ideology [Ahn et al., 2014]. The finding in this study provides important links between disgust sensitivity and racial prejudice, indicating traits, such as disgust sensitivity, might serve to structure complex human social systems [Schaller and Park, 2011].

Nevertheless, it should be noted that the current study has some limitations. Given the nature of passive viewing task, participant might guess that the experiment was intended to assess their reactions to race. It is possible that instead of indicating a threat response of foreign faces, the increased engagement of amygdala and visual cortex might represent the threat of social evaluation [Amodio, 2014], i.e., participants worried that they would be judged as racists. Further studies are needed to differentiate the two distinct roles that amygdala might play in racial face perception.

In sum, the current findings provide direct evidence that the insula is largely involved in racially biased perception of facial disgust through two distinct neural pathways—one is automatic amygdala-based emotional circuit and the other is deliberate ACC-based regulatory circuit.

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